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PHYSIOLOGICAL AND AGRONOMICAL RESPONSES OF VEGETABLE CROPS TO HEAT STRESS: A COMPREHENSIVE REVIEW

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ABSTRACT

As global temperatures continue to rise, heat stress (HS) has become an important abiotic constraint limiting vegetable crop productivity and food security. High temperatures have a detrimental impact on the physiological processes and agronomic performance of vegetable crops, particularly at critical growth stages such as flowering and fruit set. This comprehensive review highlights important mechanisms driving heat-induced damage and adaptive responses, synthesising current information on the physiological and agronomical responses of vegetable crops to HS. Physiologically, the overproduction of reactive oxygen species (ROS) caused by elevated temperatures disrupts the balance between respiration and photosynthesis, impairs water relations, causes oxidative stress, alters hormonal balance and source-sink relationships, destabilises cell membranes and denatures proteins, all of which have an impact on plant growth and productivity. Key survival mechanisms include activation of heat shock proteins (HSPs) and molecular chaperones, and accumulation of suitable solutes, such as proline. Agronomically, HS results in reduced vegetative growth, poor reproductive development, yield losses and diminished quality attributes. Furthermore, the review addresses the intrinsic variability in heat tolerance among vegetable species and genotypes, and highlights the importance of physiological traits as reliable indicators for identifying heat-tolerant cultivars. Developing successful mitigation plans, breeding initiatives and climate-resilient vegetable production systems requires a thorough understanding of the intricate interactions between physiological processes and agronomical outcomes under HS.
***Keywords*:** Climate change, heat stress, high temperature, plant adaptation, reactive oxygen species.

Introduction

Heat is one of the most devastating abiotic stresses that negatively affects agricultural productivity and global food security (Lesk *et al.*, 2016). For every 1 ℃ increase in the seasonal temperature, crop yields decrease by 10-17% (Lobell *et al.*, 1980). With the global mean temperatures predicted to rise by 0.2 ℃ per decade, the impact of heat on global food production will only worsen (Solomon *et al.*, 2007). Temperatures are rising much faster in some parts of the world, and heat waves are set to increase in intensity and duration (Alexander *et al.*, 2006). Heat

stress (HS) has been defined as the increase in temperature for a period of time higher than a threshold level, that permanently affects plant growth and development. It is a complex phenomenon that is influenced by the rate of increase of temperature, the degree of temperature elevation (intensity) and the total duration. The intensity of HS in a particular climatic zone is primarily influenced by the frequency of heat shocks and the duration of high day/night temperature (Alsamir *et al.*, 2021).

Elevated temperatures have an adverse effect on a number of vital physiological processes in plants, including photosynthesis, respiration, water relations and nutrient uptake, thereby impairing overall crop growth, yield and quality. One of the effects of high temperature is an increase in the production and accumulation of reactive oxygen species (ROS), which damage cell membranes, proteins and other macromolecules (Vacca *et al.*, 2004). High temperatures also have an impact on photosynthesis, which results in reduced carbon assimilation due to a decrease in RuBisCO activation (Busch and Sage, 2017). Additionally, heat alters the properties of cell membrane, which in turn affects membrane-binding proteins (Bita and Gerats, 2013; Sharkey and Zhang, 2010). It is believed that photosystem II (PSII) is particularly sensitive to HS. In addition to carbon assimilation, HS has been demonstrated to disrupt carbon translocation from source to sink tissues (Pressman *et al.*, 2006). Sucrose must be continuously transported from source leaves to developing reproductive tissues. HS-induced disruption of the sucrose supply and/or its breakdown into hexoses has been shown to result in male sterility and aborted seed set in tomato, indicating a severe detrimental effect of HS on the carbon balance of a plant (Pressman *et al.*, 2002).

Plants have developed several dynamic responses at the morphological, physiological and biochemical levels, that can ameliorate the harmful effects of heat stress. For instance, an overexpression of the ROS scavenging machinery transforms the ROS into less harmful molecules (Driedonks *et al.*, 2015). Additionally, ROS can activate heat shock factors (HSFs) by acting as a signalling molecule (Miller and Mittler, 2006). These HSFs bind to palindromic motifs in the promoter of heat-responsive genes, including heat shock proteins (HSPs). The classical plant hormones, including auxins, abscisic acid, cytokinin, salicylic acid, jasmonic acid, ethylene and brassinosteroids, combine external stimuli and endogenous signals to regulate the defensive response of plants to a variety of abiotic stresses, including heat (Li *et al.*, 2021). In addition to implementing these thermotolerance strategies, many protective mechanisms have evolved which enhance the cooling ability of leaves by accelerating transpiration rates (Crawford *et al.*, 2012).

Vegetables are an indispensable part of the human diet and provide us with essential vitamins, minerals, dietary fibre and bioactive phytochemicals. They are referred to as “protective foods”, and play a critical role in combating “hidden hunger” or micronutrient deficiencies. Vegetable crops exhibit a higher degree of vulnerability to HS compared to many cereal crops due to their high moisture content, delicate reproductive structures and specific requirements for pollination and fruit/seed set. As global temperatures continue to rise, there is an urgent need to facilitate the selection and development of climate-resilient and heat-tolerant vegetable genotypes. While previous literature has focused heavily on staple grains, the specific physiological and agronomical nuances of vegetable crops require dedicated attention. Thus, the primary objective of this review is to synthesise the current understanding of how HS alters the physiological and agronomical profiles of important vegetable crops, and how these crops respond to HS.

Physiological responses of vegetable crops to heat stress

Water relations and stomatal behaviour

Vegetables, being succulent products by definition, generally comprise > 90% water. Thus, water greatly influences the growth, yield and quality of vegetables. HS increases leaf transpiration rates while decreasing water uptake through roots, thereby accelerating soil moisture depletion and plant water deficits. A critical factor in determining the water status of plant cells is their water potential. Plant cells can absorb water through osmosis because their water potential is greater than that of the surrounding soil (Taiz *et al.*, 2023). Similarly, leaf relative water content (RWC) is also an important indicator of water status in plants. It has been shown that high temperature influences stomatal density, pore size and stomal conductance (Sharma *et al.*, 2015; Zhou *et al.*, 2017), and changes in these traits directly affect water loss rate (WLR). In comparison to control (26/18 ℃), the RWC of tomato (*Solanum lycopersicum*) was significantly lower, while the leaf WLR was significantly higher in HS (38/30 ℃) condition (Zhou *et al.*, 2019a). High leaf temperatures (> 30 ℃) damage cell membranes and increase permeability, resulting in electrolyte leakage and loss of cellular water content (Peer *et al.*, 2020).

HS triggers the accumulation of free radicals, such as reactive oxygen species (ROS), which peroxidise membrane lipids. This affects membrane stability and increases solute leakage, impacting water retention abilities (Sachdev *et al*., 2021). High temperatures accelerate the formation of abscisic acid (ABA), which induces stomatal closure to prevent water loss through transpiration. High temperatures cause osmotic changes like increased accumulation of compatible solutes (proline, sugars etc.), which lowers leaf water potential, making water uptake into shoots more difficult under HS conditions (Kavi Kishor *et al*., 2022). An increased transpiration rate disrupts several physiological processes in plants by causing water deficiency and a decrease in water potential. Under HS conditions, plants lose more water during the day than at night (Singh *et al.*, 2017). At 40/35 ℃, C4 plants transpire more, which results in excessive water loss to the environment and reduces their water use efficiency (WUE). On the other hand, C3 plants regulate and minimise water loss by closing their stomata, which decreases photosynthesis, particularly when drought and heat stress coexist (Bisbis *et al.*, 2018).

Photosynthesis and respiration

Photosynthesis is one of the most heat-sensitive physiological processes in plants. High temperature impairs the photochemical processes in the light reaction (thylakoid lamellae) and reduces the activation of ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO), which is involved in the carbon reaction (stroma), thereby reducing the ability of leaves to fix carbon dioxide (CO_2), and ultimately decreasing the net photosynthetic rate (P_N) (Yamori *et al.*, 2012; Zhao *et al*., 2020). Thus, reduced photosynthesis occurs under HS conditions due to the limitations of high temperature on both the light and carbon reactions of photosynthesis (Zhao *et al*. 2020). Photosystem II (PSII) is the most heat-sensitive component in the photosynthetic apparatus, and its liability is a primary limitation of photosynthesis at high temperature (Hasanuzzaman *et al.*, 2013; Szymańska *et al*., 2017). Both the donor and acceptor sides of the complex are affected when PSII is thermally inactivated at high temperatures. HS affects the oxygen (O_2)-evolving complex on the donor side, preventing water oxidation and reducing O_2 evolution, while it inhibits electron transport on the acceptor side. Under high temperatures, these combined effects cause a significant drop in PSII efficiency (Zandalinas *et al.*, 2022). For instance, exposure of potato to HS for 12 to 20 h reduced the photochemical efficiency of PSII by 88% (Kim *et al.*, 2010). In a similar vein, heat-susceptible genotypes of cucumber (*Cucumis sativus*) exhibited a predominant alternation in PSII at temperatures > 40 °C (Ali *et al.*, 2019). Chlorophyll *a* fluorescences are a useful tool for studying heat tolerance in various plants *in vivo*, as they promptly and accurately detect damage in PSII. The maximum quantum efficiency of PSII (F_v/F_m) is a significant measure of chlorophyll *a* fluorescence, and plants exposed to HS often exhibit a decrease in F_v/F_m, which may be an important indicator of heat damage and indirectly imply a decrease in P_N (Sharma *et al.*, 2015). Therefore, changes in the P_N and other photosynthetic parameters under high temperatures can be studied to judge the heat resistance of plants.

High leaf temperatures alter stomatal functions and conductance, preventing inner leaf cooling and CO_2 diffusion into carbon fixation sites (Menzel, 2024). In addition, HS influences the structure of chloroplast as well as the thermal stability of components of the photosynthetic system, reducing the activity of RuBisCO, amounts of photosynthetic pigments (chlorophyll, carotenoids), key proteins and carbon fixation capacity (Zhang *et al.*, 2022). For instance, high temperature reduced the content of photosynthetic pigments, chlorophyll and carotenoids in pepper (*Capsicum annuum*), resulting in decreased photosynthetic activity (Aleem *et al*., 2020). The effect of HS on leaf photosynthesis and carbohydrate metabolism, however, varies between crop species, making it a useful indicator for identifying heat susceptible lines.

Plants respire rapidly at temperatures between 10 °C and 40 °C, but at temperatures > 50 °C, the respiratory mechanism is compromised, resulting in reduced respiration, which in turn reduces photosynthesis, and negatively affects the ratio of the two (Bisbis *et al.*, 2018). Even in high temperatures, plants keep their respiration rates low. A study revealed that spinach grown at 15/10 °C had higher respiration rate compared to that grown at 28/18 °C in all the treatments (Bisbis *et al.*, 2018). HS may also disrupt the carbon balance in the plant due to a reduced supply of carbohydrates caused by a decline in leaf photosynthetic yield and an increased demand of carbohydrates owing to increased dark respiration and photorespiration (Vasseur *et al.*, 2011). For example, increased photorespiration rate and decreased quantum efficiency of PSII and net photosynthetic rate were observed in pepper under HS (45/35 °C) conditions compared to control (28/18 °C) conditions (Hu *et al.*, 2010a). Photosynthetic rate largely depends on RuBisCO activity, which increases the CO_2 : O_2 in the chloroplast in response to elevated CO_2 (eCO_2), thereby improving carboxylation efficiency and

suppressing photorespiration. Besides protecting chloroplasts from oxidative damage and lowering H_2O_2 production, reduced photorespiration under eCO_2 enhances photosynthesis and heat tolerance of PSII under moderate HS. However, developmental stage and other limiting factors like nitrogen availability affect the long-term benefits of eCO_2 under high temperatures. It is also important to note that HS during anthesis and post-anthesis often overrides eCO_2-induced gains and results in yield reductions despite maintained photosynthetic maintenance (Zhang *et al*., 2023).

Oxidative stress

Plants exposed to HS show overproduction and accumulation of reactive oxygen species (ROS), such as singlet oxygen ($^1O_2$), superoxide anion radical ($^{\cdot}O_2^-$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($^{\cdot}OH$), which generate oxidative stress, resulting in altered cellular metabolism, cell membrane damage, increased lipid peroxidation, inactivation of oxygen-evolving complex and nicking of DNA, all of which reduce cell viability and ultimately lead to programmed cell death (Hasanuzzaman *et al.*, 2013; Nosaka and Nosaka, 2017; Wang *et al.*, 2016). ROS are byproducts of various metabolic processes, including photosynthesis and respiration, and are mostly produced in PSII and PSI. Excess energy in PSII causes chlorophylls to enter the triplet state, which transfers excitation energy to O_2 to produce $^1O_2$. Over-reduction of PSI leads to production of $^{\cdot}O_2^-$, which increases the formation of H_2O_2 (Szymańska *et al.*, 2017). Among the ROS, $^{\cdot}O_2^-$ is the first to be produced, whereas H_2O_2, due to its high membrane permeability and relatively long half-life, works as oxidative burst signal. In tomato, H_2O_2 content is a well-established index of oxidative stress (Sánchez-Rodríguez *et al.*, 2010). An excessive accumulation of ROS under HS can cause protein denaturation and misfolding in plant reproductive organs, which can impede normal cellular processes and contribute to reproductive failure (Bao *et al.*, 2024).

Conversely, plants have evolved systems that improve heat tolerance and detoxify ROS. Plants improve their thermotolerance by recruiting antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR) and peroxidase (POX) (Jespersen, 2020). SOD is generally considered the first line of enzymatic defense against ROS, which catalyses the dismutation of the $^{\cdot}O_2^-$ into O_2 and H_2O_2, thereby reducing oxidative stress in cells (Jomova *et al.*, 2024). Likewise, the enzymes POD, CAT and APX are highly efficient in degrading H_2O_2. While moderate HS can enhance the activity of protective antioxidant enzymes, extreme heat upsets the balance between ROS production and scavenging, resulting in an excessive accumulation of ROS and malondialdehyde (MDA) from lipid peroxidation. The content of MDA, the final production of peroxidation of unsaturated fatty acids in phospholipids, is often used as an indicator of lipid peroxidation level to evaluate the degree of cell membrane damage under HS conditions (Scandalios, 1993). Carotenoid, besides being a key component in photosynthesis, also plays an essential role as a non-enzymatic antioxidant in ROS mechanisms (Gill and Tuteja, 2010). Proline has also been documented as an osmotic adjustment mediator, stabilise subcellular structure, eliminate free radical and buffer redox potential under stress conditions (Molinari *et al.*, 2004). The dynamic changes in ROS metabolism, antioxidant enzyme activity, MDA, proline and pigment content in leaves of tomato under HS (38/30 °C) showed a significant increase in SOD and APX activities, as well as proline and carotenoid levels, while the MDA level and ROS accumulation were limited, although the results depended on the cultivars (Zhou *et al.*, 2019b). Similarly, elevated expressions of APX in tomato, GRX (glutaredoxin), CAT2 (catalase-2) and FDX (ferredoxin) in onion (*Allium cepa*), SOD, POD and CAT in cucumber, and SOD and APX in potato (*Solanum tuberosum*) were observed to activate antioxidant defence in the heat-tolerant genotypes (Galsurker *et al.*, 2018; Kim *et al.*, 2010; Tang *et al.*, 2006; Wang *et al.*, 2006). Likewise, the MDA and $^{\cdot}O_2^-$ contents increased by 60.6 and 79.9%, respectively, when cucumber seedlings were exposed to HS (35 ± 1 °C) condition (Ding *et al.*, 2016).

Cell membrane stability and integrity

Cell membrane damage induced by HS is caused by denaturation of membrane proteins, inactivation of enzymes and subsequent alterations in membrane permeability and integrity that result in increased permeability, decreased ion flux, changes in RWC, loss of pigments, production of toxic compounds, electrolyte/ion leakage and a general disturbance of homeostasis that lowers cell viability. This decreased viability leads to stunted plant growth, reduced leaf area, leaf withering and leaf abscission (Nijabat *et al.*, 2020). High temperatures exacerbate the peroxidation of cell membrane lipids, leading to disruption of the balance between the production and elimination of ROS (Ul Hassan *et al.*, 2022). Dysfunction of cell membranes in response to HS is best estimated by measure of electrolyte leakage (EL) from cell membrane in aqueous medium. In many plant species,

an increase in EL is an indirect indicator of the heat-tolerance response and a sign of disruption of cell membrane integrity (Khajuria *et al.*, 2016). For example, heat-susceptible genotypes of hot pepper showed cellular membrane damage when exposed to 35.6 °C (Ghai *et al.*, 2016). Likewise, higher membrane damage and EL have been recorded in heat-susceptible genotypes of cucumber (Ali *et al.*, 2019) and potato (Makarova *et al.*, 2018). Higher yields are typically sustained by plants with excellent cell membrane stability and RWC during HS at various growth stages, from seedling to harvest (Khakwani *et al.*, 2012).

Under HS conditions, plants synthesise greater amounts of proline, which acts as an osmoprotectant and helps stabilise the cellular structures, including membranes, thereby alleviating HS-induced damage to the cell membrane (Tiwari *et al.*, 2024). Additionally, in response to HS, a group of protective proteins, known as heat shock proteins (HSPs), are synthesised. These proteins serve as molecular chaperons that stabilise proteins and help in the preservation of cellular structures, including the cell membrane, thereby protecting the cell from HS-induced damage (Singh *et al.*, 2024). Given the critical role that the cell membrane plays in maintaining cellular integrity, measures of membrane stability, both before and after exposure to HS, provide quantifiable information that has been found to be well-correlated with heat tolerance (Wahid *et al.*, 2007).

Protein denaturation and chaperones

HS affects plant cells in several ways, such as changes in the condition of cellular membrane, structural changes in DNA and DNA, and conformational changes of proteins, cytoskeleton structures and metabolites (Mittler *et al.*, 2012; Ruelland and Zachowski, 2010). For example, high temperature modifies membrane rigidification, thereby altering membrane fluidity (Ruelland and Zachowski, 2010). HS can cause a protein to be denatured, unfolded, or misfolded (Ohama *et al.*, 2017; Scharf *et al.*, 2012), resulting in protein aggregation in cells due to interactions among the exposed hydrophobic amino acid residues of affected proteins (Nakajima and Suzuki, 2013). Plants synthesise molecular chaperons, including heat shock proteins (HSPs), which identify these hydrophobic amino acid residues in non-native proteins and facilitate the folding and refolding of denatured proteins. As molecular chaperons, plant HSPs significantly contribute to HS tolerance and help in the correct folding of target proteins by preventing denaturation and protein aggregation (Ahuja *et al.*, 2010; Jacob *et al.*, 2017). For instance, under normal temperature, heat stress transcription factors (HSFs) regulate the heat shock response (HSR) and form inactive multiprotein complexes with HSPs, while under HS, HSFs separate from the complex and create phosphorylated trimers, which enable them to translocate to the nucleus and bind to the heat shock element (HSE) to trigger target gene transcription (Ahuja *et al.*, 2010; Jacob *et al.*, 2017; Ohama *et al.*, 2017; Scharf *et al.*, 2012).

The HSPs are generally grouped into five major families based on their molecular weight, viz. HSP100 (100-104 kDa), HSP90 (80-94 kDa), HSP70 (68-75 kDa), HSP60 (57-60 kDa) and small HSPs (sHSPs; 15-42 kDa) (Gupta *et al.*, 2010). It has been demonstrated through *in vivo* and *in vitro* experiments, that sHSPs can associate with thylakoids and protect O_2 evolution and the OEC proteins of PSII under HS (Barua *et al.*, 2003; Heckathorn *et al.*, 2002). Among chloroplast sHSPs, the tomato *HSP21*, induced by heat treatment, plays a crucial part in the establishment of PSII thermotolerance by protecting PSII from oxidative stress (Neta-Sharir *et al.*, 2005), thereby highlighting the importance of HSPs in thermal protection of chloroplast. The 18 kDa sHSP proteins were reported to have been synthesised for a longer time in the heat tolerant potato cultivars as against the heat sensitive ones under HS (Ahn *et al.*, 2004). The proteins of HSP70 family are one of the most highly conserved classes of HSPs (Gupta *et al.*, 2010). In the meantime, the co-chaperones of HSP70 and HSP90 are associated with signalling, protein targeting and degradation (Jacob *et al.*, 2017). In response to HS, vegetable crops synthesise many stress-responsive proteins, including HSP, by regulating gene expression. For example, the thermotolerant line of pepper displayed significant upregulation of the *HSP70* gene after 2 h of HS (42 °C) treatment, compared to the thermosensitive line, indicating the rapid and sharp induction of the gene by heat shock and its role in thermotolerance (Usman *et al.*, 2015). Similarly, 16 *RsHSP70* genes were consistently upregulated (four to eightfold increase) under HS (42 °C, 2 d) in radish (*Raphanus sativus*) (Pan *et al.*, 2024). Recently, among the early heat responsive HSP genes identified in lettuce (*Lactuca sativa*), *sHSP* and *HSP70* genes were quickly and sharply induced within 1 h in response to HS, suggesting that these genes could serve as potential breeding targets for the development of heat-tolerant lettuce cultivars (Kang *et al.*, 2021).

Source-sink relationships

Source tissues are net producers of photoassimilates, mostly carbohydrates such as sucrose, whereas sink tissues use or store them.

Sucrose is the major carbon assimilate from photosynthesis and constitutes around 90% of plant biomass (along with H and O), and is a key factor in determining yield (Aluko *et al.*, 2021; Ruan *et al.*, 2010). In order to support the growth of sinks, such as roots, developing flowers, fruits, seeds and storage organs, sucrose is transported from source tissues (leaves) via the phloem to the sink tissues, where it is broken down into hexose or its derivatives, mainly glucose and fructose. High temperatures inhibit photosynthesis and reduce carbohydrate production in source leaves by disrupting key components of the photosynthetic machinery, including electron transport, RuBisCO activity and overall chloroplast function, leading to diminished carbon assimilation and impaired carbohydrate synthesis under HS. The progression of flowering and early fruit development accelerates under high temperatures, resulting in shortened duration of reproductive phase and limited capacity of reproductive sinks to accumulate and store carbohydrates in the developing seeds and fruits (Xing *et al.*, 2024). Under HS, source-sink relationships are severely disrupted as carbon partitioning to reproductive sinks is suppressed. This leads to reduced reproductive growth, insufficient energy supply in sink organs and yield and quality penalties (Pressman *et al.*, 2002; Suwa *et al.*, 2010). Many crops, including tomato, are more susceptible to greater temperatures at night than daytime temperatures when it comes to reproductive development. For instance, when nighttime temperatures > 24 °C, up to 80% of tomato flowers or fruits abort (Ruan *et al.*, 2010). This implies that the effects of HS may be made worse by an inadequate supply of carbon assimilates to sink organs at night. Unfortunately, compared to daytime warming, nighttime warming is now more common worldwide (Cox *et al.*, 2020). Elevated temperatures downregulate cell-wall invertase (CWIN) expression (e.g., LIN5 in tomato), leading to reduced sucrose cleavage in sink organs, accumulation of sucrose and deficiency of hexoses required for growth. This decreases sink strength, causes fruit abortion and prevents source-to-sink transport despite largely unchanged photosynthetic source activity (Lou *et al.*, 2025). Therefore, to sustain vegetable productivity under high temperatures (or HS conditions), crop improvement and management strategies should be in line with the physiological mechanisms that regulate source-sink relationships.

Hormonal balance and signalling

HS significantly alters growth, reproductive development and stress adaptability in vegetable crops by disturbing hormonal balance and signalling. The potential involvement of a hormone in response to HS can be confirmed by variations in the level of that particular phytohormone and/or plant tolerance in response to high temperatures. Complex hormone signalling pathways under HS have been largely unravelled by advanced studies that use sophisticated molecular techniques in combination with functional analysis through the generation of impaired mutants or overexpression of a specific gene involved in hormone biosynthesis and/or signalling. However, the response varies with the plant stage (vegetative or reproductive) during which HS is imposed (Mittler *et al.*, 2012). Several hormones that were previously solely recognised for their functions in plant growth and development have recently been linked to how plants respond to HS because of the on-going advancements in molecular technologies (Dobrá *et al.*, 2015). In addition, hormonal cross-talk has also become much more complex due to the involvement of several hormones that fine-tune plant response to HS. Because of the extensive cross-talk among hormone networks, a summary of how HS regulates hormone biosynthesis and signalling in different vegetable crops has been presented in Table 1.

Auxins, gibberellins (GAs), abscisic acid (ABA), cytokinins (CKs), ethylene (ET), salicylic acid (SA), jasmonic acid (JA) and brassinosteroids (BRs) are among the primary phytohormones (Xia *et al.*, 2015; Zhou *et al.*, 2014), the production and signal transduction of which are modulated by elevated temperatures, usually in a tissue- and developmental stage-specific manner. Under HS, the levels of stress-related phytohormones, such as ABA, JA, SA and ET generally increase, whereas those of growth-promoting hormones, including auxins, GAs and CKs, decreases, indicating a shift from growth to stress-adaptive responses (Waadt *et al.*, 2022). For instance, in garlic (*Allium sativum*) the growth-promoting hormones, auxin (IAA) and gibberellic acid (GA_3), significantly decreased during the early stages of HS (IAA and GA_3 levels were 60.35% and 49.10% lower, respectively, at 4 h than at 0 h), while stress-response hormones, including ABA, JA, SA and ET, increased (Yang *et al.*, 2025). The (GA_3 + IAA) : ABA also decreased rapidly from 0 to 4 h of HS but increased somewhat after 24 h, suggesting the potential adaptation ability of garlic leaves to HS based on hormone balance.

Abscisic acid (ABA) is one of the most extensively studied phytohormones involved in regulating HS responses, and is required during most of the developmental stages to induce heat tolerance. HS induces a rapid increase in the endogenous ABA concentration, which induces stomatal closure in leaves

and acts as a signalling molecule for the activation of many HS-related genes. ABA serves as a heat-initiating hormone, making heat shock reactions faster and more effective, and enhancing the antioxidant ability to confer heat tolerance in plants (Hu *et al.*, 2010b; Hu *et al.*, 2018; Li *et al.*, 2021). For example, the partially ABA-deficient tomato mutant genotype, *notabilis* (*not*), was found sensitive to HS (42 °C for 24 h) as evidenced by decreased photochemical efficiency (F_v/F_m) and increased lipid peroxidation compared to the wild-type, *Ailsa Craig* (Li *et al.*, 2015). Likewise, the ABA levels rapidly increased following exposure of pea plants to HS (38 °C for 2 h), as early as 10 minutes, indicating its involvement in heat sensing and acclimation (Liu *et al.*, 2006). ABA is also documented to induce HSP70 protein under HS conditions (Hu *et al.*, 2010b). For instance, in cucumber grafted on luffa (*Luffa cylindrica*) rootstock (*Cs*/*Lc*), by up-regulating *RBOH* (Respiratory Burst Oxidase Homolog) expression, the enhanced ABA accumulation in the leaves stimulated H_2O_2 production, which in turn promoted the accumulation of HSP70 and subsequent heat tolerance in response to HS (25/40 °C (root zone HS), 40/25 °C (aerial HS) and 40/40 °C (combined HS) shoot/root temperature). Furthermore, the exogenous application of ABA improved heat tolerance in *Cs*/*Cs* (cucumber grafted on cucumber) plants, underscoring the involvement of ABA in heat tolerance (Li *et al.*, 2014).

The plant hormone ethylene (ET) is a key regulator of abiotic stresses responses and its accumulation, at different concentrations, is linked to the plant responses to abiotic stresses, including HS (Khan *et al.*, 2020). HS regulates ET production primarily in the reproductive tissues such as pedicel and fruit tissues and optimises the dynamics of resource allocation (Savada *et al.*, 2017). By activating a number of stress-related proteins involved in maintaining functional integrity of plant cells, exogenous application of ET (such as ethephon) contributes significantly to thermotolerance (Jegadeesan *et al.*, 2018). ET signalling is also involved in the mitigation of HS-induced adversities in plants and enhancement of thermotolerance by lowering oxidative stress and maintaining chlorophyll content. Moreover, HSPs and genes related to ET signalling are involved in the sophisticated network of signal transduction for thermotolerance (Wu and Yang, 2019). As a gaseous hormone, ET has dose- and time-dependent effects on plants under HS. While a low concentration of ET helps plants active defense signalling in plants, its high concentration appears to be inhibitory in cucumber during post-harvest storage (Chang *et al.*, 2010). ET production and signalling during HS has been associated with the onset of leaf senescence and a decrease in traits like pollen germination, pollen tube growth, fruit set and others. For instance, a study revealed that perturbation of the tomato ET signalling pathway, by a mutation in the ethylene response sensor (ERS)-like ET receptor, affected pollen carbohydrate metabolism and increased the severity of pollen grains to MCHS (mild chronic HS; 32/26 ± 2 °C) conditions, as shown by a decrease in the total number of pollen grains produced, an increase in the number of non-viable pollen grains and a significant reduction in the number of viable pollen grains in ET-insensitive mutant *Never ripe* (*Nr*) plants. Conversely, application of an inhibitor of ET biosynthesis affected both basal and acquired thermotolerance in pollen, as reflected by a reduction in the number of germinating pollen grains, thus highlighting the role of ET and ET signalling pathway in maintaining high pollen quality under HS conditions (Firon *et al.*, 2012). High temperatures, particularly in the range of 30-38 °C, have been documented to induce an increase in the ET production in tomato (Pan *et al.*, 2019) and common bean (Sauter *et al.*, 1990), however, inhibition of ET has also been observed in tomato at 40 °C (Biggs *et al.*, 1988).

Free jasmonic acid and one of its derivatives, the active precursor compound, 12-oxy-phytodienoic acid (OPDA), are collectively referred to as jasmonic acid (JA). Additionally, methyl jasmonate (MeJA) and jasmonoyl-l-isoleucine (JA-Ile) are its primary derivatives. JA is a crucial lipid hormone in plants that influences anthocyanin accumulation, trichome development, stamen production, seed germination, root growth, leaf ageing (senescence), flowering duration and plant defence responses to biotic and abiotic stresses (Ruan *et al.*, 2019; Shikha *et al.*, 2023; Wang *et al.*, 2021). Some immature and mature plant tissues produce JA, which controls how plants react to external environmental challenges like drought, high and low temperatures, ozone, and UV radiation. Research has confirmed that MeJA can stimulate terpene production in plants and is involved in cucumber stomatal closure (Gomi, 2021). Salicylic acid (SA) is a naturally occurring phenolic phytohormone that encourages plant growth and development, and stimulates defense mechanism. The crucial role of SA in regulating plant responses to a variety of abiotic stresses, including HS, is well-documented. For instance, foliar application of SA enhanced the activity of antioxidant enzymes in tomato, stabilising membrane damage and reducing the impacts of HS (Jahan *et al.*, 2019). Similarly, SA considerably increased the heat tolerance of chilli plants exposed to HS (42 °C, 72 h) by enhancing

antioxidant activity and membrane integrity (Saeed *et al.*, 2023). Brassinosteroids (BRs) are a group of plant-specific steroidal hormones, and are important signalling molecules regulating plant growth and development, and defense response (Manghwar *et al.*, 2022). Several studies have demonstrated that exogenous BRs can enhance abiotic stress resistance in many plant species (Zhou *et al.*, 2014). For example, a study revealed that application of BRs significantly increased the TSS content and antioxidant capacity to maintain stomatal openings and protect photosynthetic apparatus in tomato under HS (Ogweno *et al.*, 2008). Auxin plays an important role in high-temperature-induced thermomorphological changes, such as stem elongation and leaf water loss (Li *et al.*, 2021). Likewise, GAs promote cell wall relaxation and cell elongation, resulting in stem elongation, which plays a major role in the bolting of vegetables (Richards *et al.*, 2001). Results from a study revealed that the contents of ABA, GA_{1+3}, zeatin (ZR), auxin (IAA), jasmonic acid methyl ester (JA-ME) and BR were significantly higher in the bolted stems of lettuce plants subjected to HS (33/25 °C), and there was a stronger significant difference in IAA than in ABA, GA_{1+3}, JA-ME and BR, suggesting that exogenous IAA increases bolting (Hao *et al.*, 2018). From the study of changes in hormonal pathways, it was speculated that the increased abundance of proteins involved in GA and IAA metabolism increased the content of endogenous GA and IAA, thereby enhancing photosynthesis and promoting bolting. Collectively, these findings underscore that HS-induced hormonal balance and signalling in vegetable crops is governed by a complex crosstalk among growth- and stress-related hormones, ultimately determining heat-tolerance and yield stability.

Table 1 : Effects of heat stress on plant hormone biosynthesis, accumulation and signalling in different vegetable crops.

Vegetable crop	Heat treatment	Plant hormone	Effect	References
Cucumber	40 °C vs. 25 °C	ABA	(↑) ABA level and transport	(Li *et al.*, 2014)
Lettuce	30 °C vs. 20 °C	Auxin	(↑) expression of genes involved in auxin biosynthesis and tryptophan metabolism	(Hao *et al.*, 2018)
	35 °C vs. 20 °C	ABA	(↑) ABA level and biosynthetic gene expression	(Argyris *et al.*, 2008)
	35 °C vs. 20 °C	Ethylene	(↓) ethylene biosynthetic gene expression	(Argyris *et al.*, 2008)
	35 °C vs. 20 °C	Ethylene	(↑) or (↓) ethylene response factor ERF1 gene expression depending on the genotype	(Yoong *et al.*, 2016)
Pea	33-35/17 °C vs. 19/17 °C	Ethylene	(↑) ethylene level in pre-pollinated ovaries but (↓) levels in ovaries, stigma, style and petals after pollination	(Savada *et al.*, 2017)
Pepper	24 °C vs. 20 °C	SA	(↑) SA levels and immunity	(Koeda *et al.*, 2012)
Tomato	35/30 °C vs. 25/20 °C	JA	(↓) JA and JA-Ile levels in stamens and (↓) JA levels in pistils leading to stigma exsertion	(Pan *et al.*, 2019)
	45 °C vs. 25 °C	Ethylene	(↑) ethylene level and biosynthetic gene expression	(Jegadeesan *et al.*, 2018)
	45 °C vs. 25 °C	Ethylene	(↑) ethylene receptor ETR3 and signalling gene CTR2 expression	(Jegadeesan *et al.*, 2018)

(↑) Increased, (↓) Decreased, *ABA* Abscisic acid, *ERF1* Ethylene Response Factor 1, *JA* Jasmonic acid, *JA-Ile* Jasmonyl-Isoleucine, *SA* Salicylic acid

Agronomical responses of vegetable crops to heat stress

Implications of heat stress on crop growth and yield

Heat stress (HS) significantly alters the growth, development and productivity of vegetable crops by accelerating phenological changes and disrupting key reproductive processes. Exposure to high temperatures often forces plants to complete their life cycle rapidly, a phenomenon known as “phenological squeezing”, which prevents adequate biomass accumulation and compromises marketable yield. This is particularly destructive in cool-season vegetables, where even slight increases in temperature can trigger irreversible developmental abnormalities. For instance, a temperature range of 15-18 °C is considered optimal for Chinese cabbage (*Brassica rapa* ssp. *pekinensis*) at heading stage, and a mean temperature > 25 °C usually hinders leaf head formation. Therefore, the production of Chinese cabbage is threatened by HS in many regions (Song *et al.*, 2019).

In leafy vegetables, such as lettuce and spinach (*Spinacia oleracea*), the main agronomic response to HS is bolting, i.e., the rapid, premature elongation of the flowering stalk. Bolting is a survival strategy aimed at completing the reproductive cycle before the plant perishes from deadly heat, but it occurs at the expense of vegetative quality. Head lettuce cannot be sold at all, while leaf lettuce and spinach become tough and bitter-tasting. HT conditions in lettuce and cilantro (*Coriandrum sativum*) accelerate bolting, which affects the flavour, limits crop marketability and renders the produce (leaves) unpalatable for consumers (Chen *et al.*, 2022; Meyering *et al.*, 2020). High incidence of pre-harvest bolting in open-field or protected condition can cause significant economic loss. Moreover, accelerated phenology forces farmers to harvest small, immature plants to prevent quality loss, which significantly reduces the overall leaf yield per hectare.

The transition from flowering to fruit set represents the most critical bottleneck for vegetable productivity under a warming climate. Reproductive organs are far more sensitive to temperature fluctuations than vegetative tissues. Pollen is the most heat-susceptible tissue in many crops (Giorno *et al.*, 2013), and in the absence of viable pollen, the fruit set is reduced or completely impeded in solanaceous fruiting vegetables. HS negatively affects growth and fruit production in tomato by reducing pollen viability, increasing the chances of flower abortion, and decreasing fruit set, weight and seed count (Paupière *et al.*, 2017; Pham *et al.*, 2020; Rieu *et al.*, 2017). Temperatures > 32 °C cause various anatomical distortions, the most notable being style exsertion. In this condition, the stigma protrudes out of the anther cone, thereby impeding self-pollination and fruit-set, and reducing productivity (Amrutha *et al.*, 2023; Xu *et al.*, 2017). Although vegetative growth in chilli pepper remains considerably unaffected, HS shows detrimental effects during reproductive stages (Srivastava *et al.*, 2022). Exposure to HT inhibits one or more post-pollination events, such as stigma receptivity, pollen germination, growth of pollen tube towards the ovary and/or fruit initiation and development in bell pepper (Erickson and Markhart, 2002). These results demonstrate how the reproductive processes in solanaceous vegetables are disproportionately sensitive to HS.

Leguminous vegetables exhibit substantial loss of seed yield under HS during reproductive phase, mainly by compromising seed setting and/or subsequent seed filling. It is important to note that failure of seed setting by HS imposed at the early reproductive stage cannot be revived, resulting in severe and irreversible yield loss, while seed filling compromised due to HS imposed at the late reproductive stage may be, to some extent, recovered by following proper management practices. HS just prior to or during flowering usually has the most detrimental effect on seed setting in legumes. The germination rate of pollen grains in common bean (*Phaseolus vulgaris*) has been reported to decrease by 52% due to HS (32/27 °C) (Porch and Jahn, 2001). High night temperature (27 °C) impaired anther dehiscence in common bean (Konsens *et al.*, 1991), while in cowpea (*Vigna unguiculata*), high night temperature (30 °C) resulted in small and shrunken pollen, and ultimately, 100% pod abortion (Ahmed *et al.*, 1992). Common bean genotypes showed reduced yield mass, seed set and pod set when exposed to day temperatures of 32 °C during the flowering phase (Porch and Jahn, 2001). Similar response to HS has been documented in pea (*Pisum sativum*) at 30 °C (McDonald and Paulsen, 1997). On exposure of faba bean (*Vicia faba*) to HS conditions, there was a reduction in total yield, mass per bean and pollen germination (Bishop *et al.*, 2016). The reduction in yield due to HS is often caused by a combination of reduced pod and seed set, highlighting post-stress problems in fertilisation. Thus, the main cause of HS-induced yield losses in leguminous vegetables is disruptions in fertilisation rather than vegetative growth limitations.

In a similar vein, HS strongly alters the sex expression in cucurbitaceous vegetables, leading to an increase in the ratio of male to female flowers and consequently reducing the number of fruits per plant and overall yield. Early studies demonstrated that squash (*Cucurbita pepo*) grown under controlled environmental conditions at a mean temperature of 30 °C produced up to 160 nodes without a single pistillate flower (Nitsch *et al.*, 1952). Meanwhile, when the temperature was reduced, particularly at night, female flowers appeared on nodes 20 to 30 on the main stem. Extreme temperatures (42 °C) suppress seed germination in cucumber, thereby impairing vegetative and reproductive growth. HS during fruit development causes bitterness in the fruit (Kumar *et al.*, 2011). Pollen from bottle gourd (*Lagenaria siceraria*) flowers subjected to HT (38 °C) for 7 h failed to germinate and grow into the styles of female flowers, thereby failing to induce fruit-set (Iapichino and Loy, 1987). Thus, prolonged exposure to high temperatures (> 36 °C) can inhibit fruit-set drastically and reduce yield in bottle gourd. Improper or incomplete fertilisation due to poor pollen viability in cucurbits often results in crooked or misshapen fruits that fail to meet market standards. These reproductive failures can lead to a 70-90% reduction in harvestable yield even if the vegetative

growth of the plant appears healthy.

Vegetables that are harvested for their underground storage organs are particularly vulnerable to elevated soil temperatures, which often exceed air temperatures in poorly irrigated or plastic-mulched systems. Potato is a heat-sensitive crop, and high temperature is one of the most important uncontrollable factors affecting potato yield (Raymundo *et al.*, 2017; Trapero-Mozos *et al.*, 2018). For most of the commercial potato cultivars, the optimum temperature range for tuber bulking is 14-22 °C (Struik, 2007), but when air temperatures exceed 25 °C and soil temperatures rise above 18 °C, tuber initiation and growth are hindered. The process of tuberisation is controlled by the SP6A protein, which is produced in leaves and transported to stolons via phloem (Hastilestari *et al.*, 2018; Lehretz *et al.*, 2019). However, HS conditions inhibit the expression of this protein, effectively preventing the plant from forming tubers (Lehretz *et al.*, 2019). High temperatures ≥ 25 °C redirect the photo-assimilates to the haulm, shoot growth and root growth, leading to reduced tuber size and tuber number, and ultimately, reduced tuber yield (Trapero-Mozos *et al.*, 2018). Some of the detrimental physiological effects of HS on this crop include reduced early sprouting, uneven-shaped tubers, more small-sized tubers, bitter and toxic tuber formation, low quality tubers with less dry matter, pre-harvest sprouting, increased plant height, reduced stem thickness, increased concentration of reducing sugars and increased susceptibility to diseases (George *et al.*, 2017; Hastilestari *et al.*, 2018; Tang *et al.*, 2018). Elevated temperatures can cause heat sprouting or field sprouting, where immature tubers in the soil begin to produce new vegetative shoots (sprouts) while still attached to the mother plant, preventing starch storage and diminishing the commercial value of the crop (Zhang *et al.*, 2021).

Implications of heat stress on quality of vegetables

Vegetable quality traits may be broadly classified into three main categories, viz. commodity quality or market value, which focuses on appearance, freshness and consistency; sensory value, which covers flavour, texture and taste; and nutritional quality, which includes both essential nutrients (vitamins, minerals, dietary fibre and bioactive compounds) and undesirable substances (nitrates, glycoalkaloids, pesticide residues etc.) (Gao *et al.*, 2022). Temperature has a significant impact on the nutritional value of vegetable produce as it influences the rates of all chemical and biochemical reactions (Jung *et al.*, 2023). Elevated temperature or HS can significantly increase the biosynthesis and concentrations of certain secondary metabolites, particularly flavonoids and phenolic compounds, attributable to their function as antioxidants in protecting plants from HS (Chai and Schachtman, 2022). The shelf life, post-harvest physiology and nutritional composition of vegetables are all affected by HS that occurs during crop production. High temperatures during growth alter source-sink relationships, antioxidant systems and metabolite partitioning, making tissues more susceptible to moisture loss, accelerated senescence and quality deterioration during storage and transport. As a result, the agronomic effects of HS result in substantial post-harvest nutritional and functional losses.

In leafy and cruciferous vegetables (e.g., lettuce, Chinese cabbage, broccoli etc.), high night temperatures have been reported to increase the incidence of tipburn disorder (Saure, 1998). Likewise, temperatures > 17-28/3-12 °C (day/night) increased the incidence of loose and puffy heads, tipburn and leaf chlorosis in head lettuce, with an accumulation of bitter compounds (Wien, 1997). Among cruciferous vegetables, broccoli (*Brassica oleracea* var. *italica*) thrives in moderate temperatures (5-25 °C) (Hatfield and Prueger, 2015), with an optimal range of 15-23 °C, and under high temperatures (> 25 °C), the head quality is significantly degraded, reflected by reduction in head weight and diameter, presence of leaves (bracts) between the flower buds, uneven head surface and undesirable head coloration (Björkman and Pearson, 1998; Kop *et al.*, 2003). In broccoli and cauliflower (*B. oleracea* var. *botrytis*), HS during the sensitive head/curd initiation stage leads to various developmental disorders such as bracting (the emergence of leaves through the head/curd) and riceyness, where floral buds develop prematurely, giving the head a granular, unmarketable texture.

Environmental and cultural conditions during growth interact to affect post-harvest quality and storability of potatoes. Potato genotypes grown in warmer areas consistently exhibited reduced process quality at harvest, reduced storability and greater incidence of physiological disorders, e.g., sugar ends, mottling and senescent sweetening, than those grown in cooler areas (Zommick *et al.*, 2014). HS may cause the carbohydrate metabolism to shift from starch synthesis to starch mobilisation and accumulation of sucrose and reducing sugars, leading to “sweetening” of the tubers. According to a study, exposing potato plants to 35 °C during tuberisation resulted in a 33.70%, 7.85% and 35.88% decline in total starch, amylopectin and amylose content of tubers, respectively (Feng *et al.*, 2019). However, the

accumulation of reducing sugars is likely due to an increase in sucrose breakdown by vacuolar acid invertase (Zhu *et al.*, 2014). The concentrations of reducing sugars (glucose and fructose) in the tubers determine the colour of fried chips (Rodriguez-Saona and Wrolstad, 1997). These reducing sugars react with amino groups in a non-enzymatic Maillard reaction to produce dark-coloured pigments when chips are fried. Low-quality potatoes are rejected by processing facilities, which puts producers at serious financial risk and could cause supply issues for processors. High tuber dry matter is considered beneficial since it reduces oil absorption during frying and increases chips recovery from the raw product. However, under HS conditions, carbon assimilation by leaves is significantly reduced, which severely restricts carbon allocation to tubers, leading to low dry matter content in tubers (Busse *et al.*, 2019).

Fruit colour plays a significant role in marketable quality of solanaceous fruit vegetables, such as tomato and pepper. The characteristic deep red colour of ripe tomato fruits is principally due to lycopene pigment. Lycopene develops best within the temperature range of 12-21 °C (Tomes, 1963). Degradation of lycopene starts at temperatures ≥ 27 °C (some sources mention 30 °C) and it is completely destroyed at 40 °C. High temperatures of 30-35°C convert lycopene into β-carotene (Hamauzu *et al.*, 1998), turning the fruits yellowish-orange that lack the deep red colour demanded by consumers. Several parameters of normal fruit ripening in tomato, including colour development, softening, respiration rate and ethylene production, are suppressed under temperatures > 30 °C (Buescher, 1979). Exposing tomatoes to 32 °C resulted in decreased quantities of lycopene, γ-carotene, violaxanthin, vitamin C, phytoene and phytofluene in comparison to those exposed to 24 °C (Hernández *et al.*, 2015), emphasising the effect of temperature on fruit pigmentation and synthesis of compounds beneficial to human health. High temperature affects red colour development in ripe chilli fruits. Furthermore, heat-stressed fruits often have thinner epidermal layers, which makes them highly susceptible to sunscald, a condition where direct solar radiation kills the surface cells, creating white, papery lesions. These serve as entry points for secondary pathogens like fungi and bacteria.

Root vegetables such as carrot (*Daucus carota*) and radish respond to HS through a change in tissue composition. To protect the vascular system from heat injury, the plant increases lignin deposition, resulting in fibrous and coarse roots that are difficult to process or eat. In radish, exposure to temperatures around 35 °C accelerates lignin production around cells, resulting in the development of cracks outside the roots (Cecílio *et al.*, 2017). Likewise, early sown (July) radish exposed to high temperature (37 °C) during the middle of the growing season exhibits higher incidence of hollowness compared to late sown (August) crop (Fukuoka and Kano, 1992). HS (> 21 °C) impairs the capacity of ascorbate glutathione cycle to detoxify ROS by reducing the ascorbic acid regeneration system, and increases polyphenol oxidase (PPO) activity, culminating in internal browning in radish (Fukuoka and Hamada, 2021). These responses illustrate how HS compromises both structural integrity and biochemical quality in root vegetables.

The results of research on the effects of HS on phytochemical contents in vegetable crops have been inconsistent, and it has been challenging to compare different studies due to the lack of a standard methodology (Table 2). For instance, a study examined the total phenolic and flavonoid contents of tomato grown in open fields (mean maximum temperature of 22.3 ± 3.9 °C) to those of fruits grown in greenhouses with and without shade over a period of four months (32.9 ± 3.1 °C to 39.1 ± 4.7 °C) (Angmo *et al.*, 2021). The total phenolic content of plants grown in the open field (54.3 ± 4.1 mg GAE/100 g FW) and greenhouse (52.4 ± 6.1 mg GAE/100 g FW) was significantly higher than that of plants grown in the shaded greenhouse (37.0 ± 4.7 mg GAE/100 g FW), as was the total flavonoid content of plants grown in the open field (16 ± 5.6 mg QE/100 g FW) compared to that in the shaded greenhouse (8.7 ± 1.7 mg QE/100 g FW). The greater synthesis of phenols and flavonoids was attributed to the higher UV radiation to which plants grown without shade were exposed. HS may, therefore, have an effect on the concentrations of potentially beneficial phytochemicals in tomato, especially in the fruit. However, the mixed results from other studies will be clarified with more research using a standard methodology.

Table 2 : Effects of heat stress on phytochemical concentrations in different vegetable crops.

Vegetable	Heat treatment	Responses measured	Effects on phytochemicals	References
Arugula and Lettuce	25 °C (36 d), 25/42 °C (20, 16 d), 25/38/42 °C (10, 10, 16 d)	Total phenolic content	(↑) total phenolic compounds	(He *et al.*, 2022)
Broccoli	38/30 °C (20 d)	Phytochemical content	(↑) total phenols, soluble sugars, carotenoids, quercetin and sinapic, ferulic, *p*-coumaric and gallic acid (↓) total flavonoids, flavonols, phenolic acids, hydroxycinnamic acids, proteins, glucosinolates and porphyrins	(Gmižić *et al.*, 2023)
Tomato	45, 50 °C (1 h per d for 7 d)	Phenolic and flavonoid content	Positive correlation with total phenolic content (↓) flavonoid content	(Alhaithloul *et al.*, 2021)
	>32 °C for > 40 d; >35 °C for 16 d	Phytonutrient concentration	(↑) β-carotene content	(Scarano *et al.*, 2020)
	32.1/24 ± 1 °C vs. 36 ± 2 °C until flower development	Lycopene concentration	(↓) lycopene content	(Vijayakumar *et al.*, 2021)
Water spinach	25, 30, 35, 40, 45 °C (96 h)	Antioxidant profile	(↑) total phenolics, flavonoids and anthocyanin content	(Wang *et al.*, 2023)

(↑) Increased, (↓) Decreased

Implications of heat stress on nutrient content in vegetables

The growth and development of vegetable plants are closely related to the establishment of a healthy root system and the availability of mineral nutrients. Several factors, such as root morphology, architecture and kinetics, and rhizospheric traits, play an important role in regulating nutrient absorption by plants (Bassirirad, 2000). The concentrations of mineral nutrients in vegetables can be strongly altered by HS. The effects on nutrient concentration differ with the exposure of plant parts to HS, such as the whole plant (root + shoot) or the roots alone. Likewise, the response varies according to the crop growth stages. Table 3 summarises the effects of heat stress on nutrient concentration in several vegetable crops.

Table 3 : Effects of heat stress on nutrient content in different vegetable crops.

Vegetable crop	Heat treatment	Change in nutrient content	References
Arugula and Lettuce	25, 38, 42 °C (36 d, R + S)	(↑) Ca and Mg (↓) K (Δ) Fe	(He *et al.*, 2022)
Cucumber	25, 32, 35, 38 °C (8 and 16 d, R)	(↑) B (↓) N, P, K, Ca, Mg, Fe and Mn	(Du and Tachibana, 1994)
Lettuce	23-38 °C vs. 20 °C (11 d, R)	(↓) NO_3^-, Ca, Cu, Fe, K, Mg, Mn and Zn	(Tan *et al.*, 2002)
Muskmelon	24, 27, 30, 33, 36 °C (9-18 d, R)	(↑) Mn, P and Zn (mg/plant)	(Klock *et al.*, 1996)
Potato	16, 20, 23, 27, 30 °C (120 d, R)	(↓) Cu and Zn at 30 °C (Δ) Cu in tuber	(Baghour *et al.*, 2002)
Tomato	24, 27, 30, 33, 36 °C (9-18 d, R)	(↓) Mn and P (mg/plant) (Δ) Zn	(Klock *et al.*, 1996)
	10, 15.6, 21.1, 26.7, 32.2, 37.8 °C (two weeks, R)	(↓) N, P, K, Mg, Mn and Zn (mg/plant) (Δ) B, Fe and Mo	(Tindall *et al.*, 1990)
Tomato and watermelon	10, 25, 35 °C (30 d, R + S)	(↑) Fe (watermelon, roots and leaves) (↓) Fe (tomato, roots and leaves)	(Rivero *et al.*, 2003)

(↑) Increased, (↓) Decreased, (Δ) No change, *R* Root, *R* + *S* Root and shoot

Thus, from the available literature, we can draw the conclusion that HS can have complex and detrimental impacts on plant-nutrient relationships. The decrease in the nutrient content during HS is caused by several factors, including reduced root growth and biomass, as well as restrictions in nutrient and water uptake (Giri *et al.*, 2017). Additionally, reduced root mass or surface area and decreased nutrient uptake per unit root are two possible explanations for the decline in nutrient acquisition during HS (Bassirirad, 2000). Furthermore, the overall effects of HS on plant-nutrient dynamics may be greatly influenced by the choice of experimental techniques, such as whole plant vs. root-only studies and intact vs. detached root-based studies.

Conclusion

The detrimental effects of HS on agricultural output are predicted to worsen in the future as a result of global climate change. Therefore, it is crucial to have a deeper comprehension of the mechanisms underlying the ability of plants to withstand HS. Exposure to either short-term HS or prolonged high-temperature stress or heat acclimation, and heat stress recurrence, is the standard approach to study how plants respond to high temperatures. Although the purpose of studying high-temperature stress is to comprehend how plants react, the actual scenario is often not reflected in the research, even when only one stress is taken into account. For instance, the temperature can change significantly during the day on a hot day. At night, it definitely decreases, giving the plants a chance to recuperate. But the following day, plants might have to deal with yet another episode of very high temperatures. Numerous studies on heat acclimation may help to explain how vegetable plants respond to HS; however, those settings often fall short of accurately simulating the temperature regimes seen in the real world. Besides, in the natural ecosystem, several biotic and/or abiotic stresses may coexist. Studying how vegetable plants/crops respond to high temperatures that are similar to those found in the real world is, therefore, very important as it could help us better understand how these crops tolerate different high-temperature challenges.

Conflict of interest

The authors declare no conflict of interest.

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